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Faunal activity in acid soils

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Abstract

Soil fauna generally have limited abilities to adapt to soil acidity. In tropical soils, invertebrates tolerate lower pH than in temperate areas and abundant and active populations may exist in soils with pH of 3.8 to 4.0. Beyond determined thresholds which may largely differ among broad taxonomic units and species, communities tend to concentrate in sites where pH conditions are more favourable, e.g. in the leaf litter or in the rhizosphere rather than in the "bulk" soil. In acid soils, the abundance of large invertebrates living either in the soil (i.e. endogeic earthworms and humivorous termites), or in burrows opening at the soil surface and in surface or subterranean nests (i.e. anecic termites and earthworms) tends to decrease. Litter-feeding arthropods and microfauna associated with the litter and rhizosphere (i.e. nematodes and protozoa) become predominant. pH is often higher in the gut of soil invertebrates than in the bulk soil; this microenvironment may be a favourable microsite for chemical reactions which are inhibited by acidity. Liming of acid soils often results in dramatic shifts in the composition and abundance of soil fauna communities. The overall biological activity is significantly increased as large endogeic and anecic invertebrates build significant populations which compete favourably with less active arthropods of the litter system. The application of high-quality leaf litter has similar effects and the decrease of the overall activity in acid soils may result from the low quality of feeding resources available rather than acidity itself. Emphasis is set on management of organic matter as a mean to sustain high levels of soil faunal activity in acid soils, and hence, increase the productivity and sustainability of cropping systems.

Introduction

Acid soils in natural conditions often host diverse and abundant invertebrate communities (Petersen and Luxton, 1982). These animals may play significant roles in the conservation of soil structure and nutrients, especially in tropical areas (Lavelle et al., 1992a). Most management practices are harmful to soil invertebrates, irrespective of their effects on soil pH, and it is believed that the destruction of soil macrofauna, especially in annual cropping systems, is an important cause for the rapid decrease of fertility in these systems (Lavelle et al., 1992b). Liming which increases pH and nitrogen fertilisation or acid depositions which acidify the soils may have significant effects on soil faunal communities.

The reason why a given soil is acid is highly relevant to the determination of the structure and activity of soil faunal communities. In the humid tropics, for example, long term pedogenetic processes have resulted in the formation of acid soils and selected acid tolerant faunas which may be abundant and active (e.g. Lavelle and Pashanasi, 1989). Similar processes occur in temperate and cold areas as acid soils develop on acid bedrocks. In the short term and on a small scale, acidification may result from the accumulation of intermediate products of the decomposition of low-quality litter (e.g. from conifers). Finally, management practices, for example, liming, nitrogen fertilisation, or the deposition of acid aerosols, may dramatically change pH over relatively short periods of time (Coleman, 1982; Ma et al., 1990).

This paper reviews the diversity and roles of invertebrates in soils. The response of communities to soil acidity is then envisaged, along a continuum of natural ecosystems and in systems which have experienced

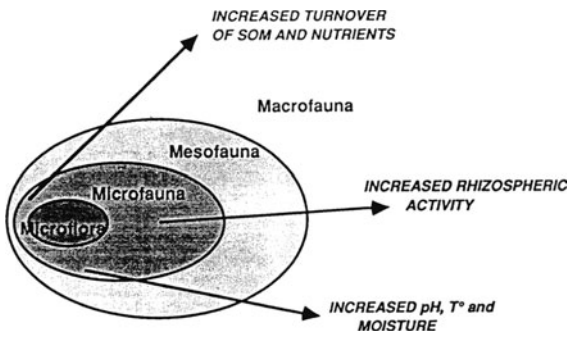

Fig. 1. Interactions among micro-organisms and macroorganisms in soils. As the size of invertebrates increases, their relationship to microflora gradually shifts from predation to external and internal mutualism. When present, larger organisms tend to be more influential over microorganisms than smaller ones, but their activity is more frequently limited by low temperature and moisture conditions.

recent changes of pH as a result of management practices. Finally the ability of soil invertebrates to modify soil acidity is considered.

Diversity and role of invertebrates in soils

Functional categories

Invertebrates living in soils face three major constraints i.e. the low quality of food resources, spatial constraints and occasional extreme conditions of temperature and moisture (Lavelle et al., 1992a).

In soils, pores only comprise a relatively low percentage of the volume. The porous space is discontinuous, partly filled with water and the size of the pores is highly heterogeneous. The size of invertebrates and the aquatic or aerial nature of their respiration, reflect their way of adapting to spatial constraints. Three groups may be distinguished:

- *Microfauna*: aquatic invertebrates <0.2mm, mainly protozoa and nematodes living in the water-filled soil pores.
- *Mesofauna*: microarthropods (mainly Collembola and Acari) and the small Oligochaeta Enchytraeidae which have an average size of 0.2–2mm and live in the air-filled pores of the soil and in the litter;
- *Macrofauna*: invertebrates >2mm. Termites, earthworms and large arthropods are the main components of this group. They have the ability to dig the soil and create specific structures for their movements and living activities (e.g. burrows, galleries, nests and chambers), also casts and fecal pellets result from their feeding activities. These organisms have been called "ecosystem engineers" for their ability to affect the soil structure and hence major soil processes via the structures that they build (Stork and Eggleton, 1992).

Microorganisms are the only group of organisms that have developed the ability to digest all the organic substrates present in soil, including the most resistant humic and tanin-proteic compounds (Gourbière, 1982, 1983; Toutain, 1985; Visser, 1985a,b). However, these organisms have extremely limited capacity to move and they may thus remain for long periods in an inactive resting stage because they are physically separated from their food resources or lack suitable microenvironment conditions. Most invertebrates have developed interactions with microflora to exploit soil resources: in these associations, invertebrates create suitable conditions for the activities of microorganisms whereas most chemical transformations are operated by the latter.

Microfauna are mainly predators of bacteria and fungi and as such play a major role in influencing population dynamics of microorganisms and releasing nutrients which have first been immobilised in microbial biomass (Clarholm, 1985; Trofymow and Coleman, 1982). This process is especially developed in the rhizosphere.

Mesofauna and large arthropods may digest part of the microbial biomass or develop mutualistic interactions in their fecal pellets: in these structures, organic resources which have been fragmented and moistened during the gut transit, are actively digested by microflora. After some days of incubation, arthropods may re-ingest their pellets and absorb the organic compounds that have been released by microbial activity. This specific type of interaction is called the external rumen type of digestion (Swift et al., 1979). Finally, larger invertebrates, like earthworms and termites, are large enough to develop mutualistic relationships with microflora inside their gut. These interactions may involve obligate (e.g. protozoa contained in the posterior pouch of lower termites) or facultative symbionts; the latter occur in the gut of higher termites and also in earthworms (Barois et al., 1987; Breznak, 1984).

Biological systems of regulation

Whenever conditions are suitable for their activities, macrofauna, and especially earthworms and termites, become dominant components of soil faunal communities. They become major regulators of microbial

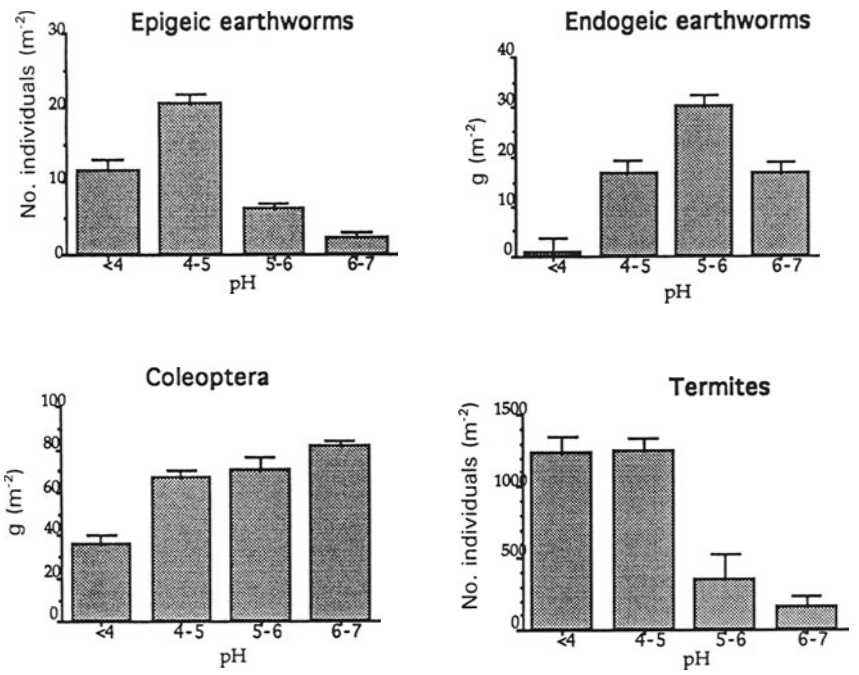

Fig. 2. Changes in abundance of major groups of soil macroinvertebrates as a function of pH in 40 tropical soils of America and Africa.

activity within their sphere of influence, in which they also determine the abundance and activities of smaller groups of soil fauna (Dash et al., 1980; Yeates, 1981). Macrofauna, however, are more sensitive than meso- and microfauna to unfavourable environmental conditions. Earthworms are the first to disappear when dry periods become too long and termites do not resist cold temperatures of temperate regions (Lavelle and Spain, 1994). As a result, in ecosystems which experience severe conditions of temperature or moisture, soil faunal communities may be dominated by large arthropods, meso-and microfauna and the overall biological stimulation of microbial activities is lower (Fig. 1).

Due to the large influence of macrofaunal components on soil structures and activities of smaller organisms, specific spheres of influence have been identified in which organisms like earthworms (in the drilosphere), termites (in their termitosphere) or large arthropods (in the litter system) regulate major soil processes (e.g. decomposition, soil organic matter (SOM) dynamics or the physical structure and hydraulic properties of soil). These "Biological Systems of Regulation" also comprise the rhizosphere in which roots are the major determinant (Lavelle et al., 1993). They influence soil processes at relatively short scales of time and space and, as such, they are themselves influenced by factors which operate at increasingly larger scales i.e., the quality of organic resources supplied to the system, edaphic (clay minerals, nutrient contents and pH) and macroclimatic factors. It is important to point out that biological regulation of soil processes becomes predominant whenever factors operating at higher levels of the hierarchy are not constraining: this is the case, for example, in some soils of the humid tropics in which neither climatic conditions, nor edaphic factors nor the quality of the organic resources produced, limit microbial activity. Similar conditions may also prevail during favourable seasons in temperate areas.

Effects on soil physical structure

Soil physical structure may be significantly affected by the activities of macro-invertebrates, especially termites and earthworms. Feeding activities are characterised by the ingestion of large amounts of soil and litter and the selective ingestion of specific organic and inorganic particles; specific structures like earthworm casts and galleries are created that may have significant effects on such processes as water infiltration, soil aggregation or resistance to erosion. For example, in African savannas of Cote d'Ivoire the annual inges-

tion of ca. 1000 t dry soil ha^{-1} by earthworms results in the deposition of 26 t of surface casts. Thirty m^3 of macropores are created inside the soil and surface roughness and surface creeping processes are significantly affected (Casenave and Valentin, 1989; Lavelle et al., 1992b). Since the vast majority of casts are deposited inside the soil they participate in the formation and conservation of a strongly macroaggregated structure. In those soils that contain <10% kaolinitic clay minerals and 1% organic matter, such a structure could not exist in the absence of faunal activities (Blanchart, 1992; Blanchart et al., 1990). Similar effects of termites have been reported in the literature (Anderson and Wood, 1984; Eschenbrenner, 1986; Garnier-Sillam, 1989; Garnier-Sillam et al., 1991; Lee and Wood, 1971a, b; Wielemaker, 1984).

Effects on SOM dynamics

Digestion processes in association with microorganisms and the subsequent egestion of organic matter into faecal pellets and casts influence the dynamics of organic matter, with different effects depending on the scale considered (Lavelle and Martin, 1992). Gut transit results in the assimilation of a significant, although highly variable, proportion of organic matter in a short time period. In earthworm casts, high concentrations of ammonium and assimilable P are found (Barios et al., 1987; Lavelle et al., 1992; Lopez-Hernandez et al., 1989; Mackey et al., 1982; Sharpley and Syers, 1976). It takes a few days to weeks until these nutrients are fully reorganised in the microbial biomass, volatilised or taken up by plants. In ageing casts, at the larger scale of time of months to years, the major effect seems to be a protection of SOM in the compact structure of casts. At the scale of the evolution of soil profile and pedogenesis (decades to centuries or more) the overall effect of earthworm activities seems to be an acceleration of the turnover rate (Martin, 1991; Martin et al., 1990).

Similar differences exist in the dynamics of SOM as affected by termite activities at different scales of time and space (Abbadie and Lepage, 1989; Garnier-Sillam and Renoux, 1989; Garnier-Sillam et al., 1987, 1988).

Effects on plant growth

Positive effects of termite and earthworm activities on plant growth have been reported on many occasions (Buse, 1990; Haimi et al., 1992; Pashanasi et al., 1992; Spain et al. 1992; Spain and Okello-Oloya,

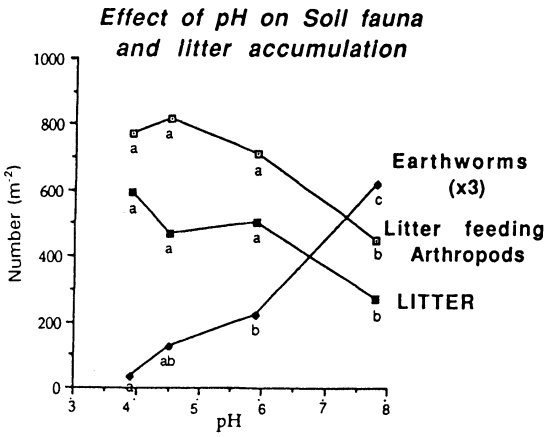

Fig. 3. Changes of pH, litter accumulation and density of macroarthropods and earthworms at Butte Montceau (Fontainebleau, France) (P Lavelle and A Faille, unpublished data) (data with different letters on a same curve are significantly different at p=0.05) (litter in g m^{-2}).

1985; Springett, 1985; Stockdill, 1959, 1982; Tomati, 1988). They are largely the result of effects of soil macrofauna and the associated meso- and microfauna and microflora, on processes of soil fertility, especially conservation of SOM and nutrients.

Response of soil fauna to acidity in natural and managed ecosystems

Range of tolerance for acidity

Soil faunal communities may be sensitive to acidity in a number of situations. Tolerance of soil invertebrates to acid pH is highly variable, even among closely related species. Nonetheless, general trends clearly appear when comparing species preferences across a wide range of situations; microarthropods and Enchythraeidae generally have maximum abundances in acid soils (pH <5) whereas nematodes and earthworms prefer slightly acid pH (5 to 6) (Petersen and Luxton, 1982).

Observations of the distribution of 65 species of earthworms across 3000 sites in France showed that epigeic species, that live and feed in the litter system, are much more tolerant to acidity than anecic (that live in subterranean burrows but regularly come to the surface to ingest litter) and endogeic species (that live in the soil and are geophagic) which clearly prefer pH of 6 to 7 (Bouché, 1972).

The composition of faunal communities is significantly affected by pH. At Butte Montceau near

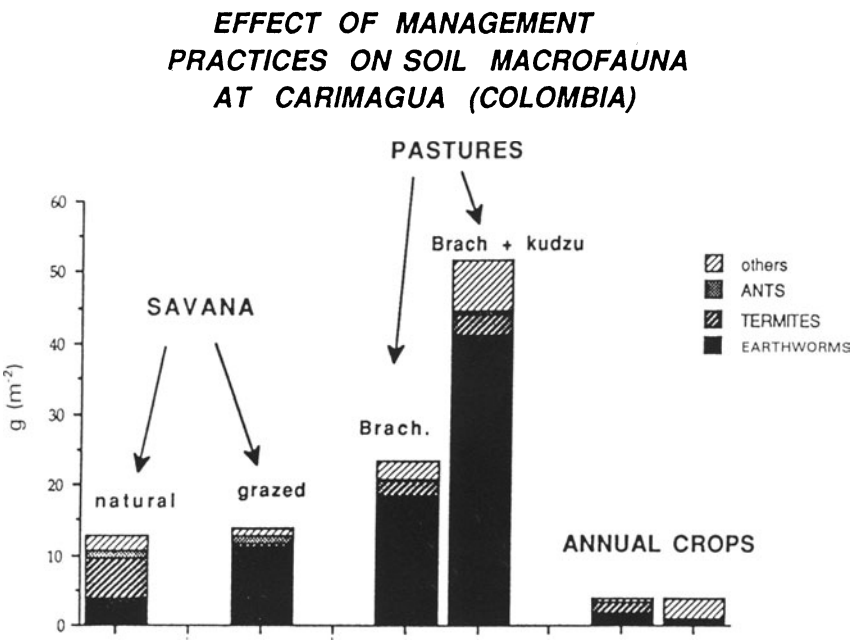

Fig. 4. Effect of management practices on soil macrofauna in Colombian Llanos (Decaens et al., 1995) (Brach.: *Brachiaria decumbens*; Kudzu: *Pueraria phaseoloides*).

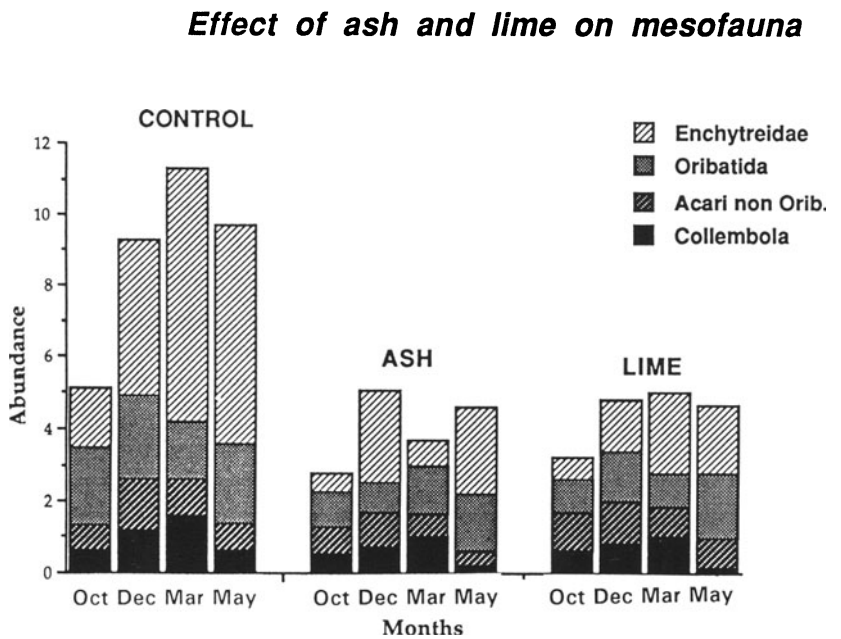

Fig. 5. Effect of application of ash and lime on mesofauna communities in a spruce stand in Finland (Huhta et al., 1986).

Fontainebleau (France), the outcrop of superimposed sand and limestone sediments along a slope creates a gradient of pH with values increasing regularly from 3.8 to 8.0 in the Al horizon, within a distance of 500 m, along which climatic conditions and composition of the tree cover are identical. At this site, acidity in the upper part of the gradient limits earthworm populations and favours the dominance of a well developed litter

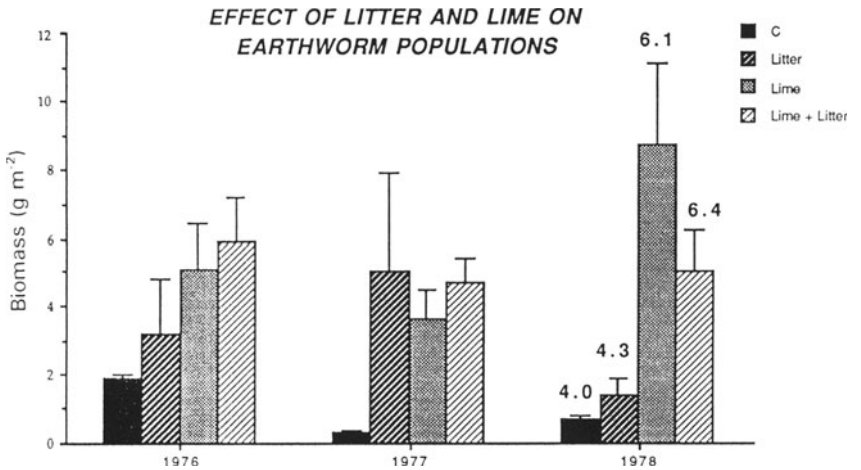

Fig. 6. Effects of application of litter and lime on earthworm populations in a spruce forest in Finland (Huhta, 1979) (inclusions on 1979 data indicate soil pH).

system with high abundance of litter arthropods (Myriapoda, Isopoda, Coleoptera and Diptera larvae) and litter accumulates as decomposition is slow (Lavelle, unpublished data) (Fig. 2). With increased pH, earthworms become more abundant and their effect on the burial of litter is significant. The drilosphere system overcomes the litter system and most faunal activity is observed inside the soil as litter is rapidly buried and decomposition is achieved inside the soil rather than in the litter system.

A survey of macroinvertebrate communities from 42 different sites in tropical America and Africa indicates clear preferences of major groups for specific ranges of pH (Fig. 3). Termites are the most tolerant to acidity with maximum abundances at pH 4 to 6, whereas ants as a group do not seem to be affected by pH and Coleoptera larvae are only abundant in soils with high pH. Earthworm abundance is also significantly related to pH. In temperate soils, epigeics have peak abundances in acid soils whereas endogeics are only abundant in soils with slightly acid to neutral pH. However, preferences of tropical species are observed at significantly lower pH values than for temperate species.

This better tolerance may explain why high earthworm and termite abundances are often observed in tropical soils with pH as low as 3.8 to 4.0. At Yurimaguas (Peruvian Amazonia), for example, the primary forest has a diverse and abundant macrofauna in a soil with a pH of 3.9. The overall density of macroinvertebrates is 4304 m^{-2} and biomass 53.9 g m^{-2}. Although earthworms comprise a large proportion of this biomass (43%), termites (18%), Myriapoda (12%) and Coleoptera significantly contribute to this community (Lavelle and Pashanasi, 1989).

Similarly in natural savannas of the Colombian Llanos (pH 4.8), macroinvertebrate communities comprise on average respectively 4290 and 2830 individuals m^{-2} in natural gallery forests and savannas (Fig. 4) (Decaens, 1993) . In these environments local variations of abundance are mainly explained by differences in soil properties and/or the quality of organic inputs. In an acid soil (pH 3.8) of tropical rainforest of French Guyana, Grandval and Leroy (unpublished data) observed a clear patchy distribution of endogeic earthworms which tend to concentrate at the foot of a tree species which produce litter with relatively low concentrations of Al and tanin complexes.

Effect of landuse practices

Management practices of acid soils in tropical environments often have dramatic effects on soil faunal communities. In both forest and savanna environments, annual crops have extremely low faunal activities despite the increase of pH brought about by slash-and-burn agricultural practices. The conversion of natural ecosystems with a thick cover into annual crops significantly alters the microclimate. Cultivation may physically damage the animals and, finally, the scarcity of fresh organic matter reduces invertebrate populations.

Conversely, pastures derived from forests or savannas may have high biomasses of soil macroinverte-

brates. Earthworms and, to a lesser extent, Coleoptera larvae are generally favoured by the high inputs of organic matter produced in the rhizosphere system or supplied as cowdung, a relatively high quality organic resource derived from above ground production. In savanna ecosystems, populations of native earthworm species are highly enhanced by this improvement of their resource base. In the Colombian Llanos, at Carimagua, the original biodiversity of the savanna is conserved in improved pastures associating *Brachiaria humidicola* and *Pueraria phaseoloides* and earthworm biomass increases from ca. 3.9 g m^{-2} in the native savanna up to 41.2 g m^{-2} (Fig. 4). Termite populations are depleted in these improved systems. In tropical forest areas, the conversion of forests to pastures may have different effects on soil fauna communities as most native species will not adapt to conditions of a grassland. In pastures derived from the Amazon rainforest at Yurimaguas (Peru), earthworm communities have a biomass of ca. 1 t fresh weight ha^{-1}. Nonetheless, this community is made of two accidentally introduced species, pantropical endogeic, *P. corethrurus* which comprises 99% of biomass, and a small epigeic *Dichogaster* originating from Africa. The activity of *P. corethrurus* is restricted to the upper 10 to 15 cm and they do not dig vertical galleries. In some circumstances, the introduction of this species has been reported to compact the soil and eventually create problems (Pashanasi et al., 1992; Rose and Wood, 1980). In other situations, the accidental introduction of adaptable species is likely to be impeded and pastures may have lowest earthworm populations. Cases of rapid degradation of pastures in Amazonia may be related to the absence of active earthworm populations. In contrast to pastures, agroforestry systems, which are combinations of trees and herbaceous plants, have a great potential to conserve and enhance native soil faunal activities in forest areas. At Yurimaguas, palm-tree plantations of *Bactris gasipaes* with a legume cover (*P. phaseoloides*) have higher biomasses of soil macroinvertebrates than the native forest. This is mainly due to the increase of biomass of a few native earthworm populations in addition to the introduction of the exotic *P. corethrurus*.

In temperate environments, there is a clear difference between soils regulated by high abundance of arthropods inside a thick litter-superficial root system, in which most decomposition operates and soils with high drilospheric effects in which most of the litter is buried and further decomposed in the soil. As observed in Figure 3 the shift from one system to another seems to be largely dependent on pH since this parameter, in a first instance, appears to be the major limitation to the spread of efficient anecic or endogeic earthworm communities (Bouché, 1972).

In spruce forests of Finland, liming and application of ash increased pH from 4–4.5 to 6.5–7.4 and resulted in significant decreases of the mesofaunal communities. In a long-term field experiment, Enchytraeidae were the most affected group and four years after application of ash, the mean biomass was only 22% of that in control soil (Huhta et al., 1986). Acari and Collembola, were differently, but less, affected. A laboratory experiment confirmed these observations on a shorter time period of 15 months (Fig. 5).

In another experiment lime and deciduous litter were applied in a spruce forest and earthworms (*Allolobophora caliginosa*) were introduced (Huhta, 1979). After two years, earthworm biomass had increased significantly in all treatments. The application of litter alone, although it resulted in only a slight increase in pH, significantly increased earthworm biomass. Three years after the last application of litter, biomass in this treatment was the same as in treatments with lime or lime + litter. One year later, biomass in the litter treatment decreased to the level of the control, probably following the complete decomposition of litter. The lime treatment had the highest biomass (g m^{-2}) (8.7 ± 2.4) followed by lime + litter (5.0 ± 1.2) litter (1.4 ± 0.5) and control (0.7 ± 0.1) (Fig. 6).

These results have been confirmed by Persson (1988) who observed a strong response of soil fauna to liming in a 40-year-old spruce stand in southern Sweden: three years after the application of lime (1.55 and 8.75 t ha^{-1}), earthworm numbers had multiplied tenfold with no significant effect of the amount of lime applied. The density of Enchytraeidae had decreased significantly to half that of the control with the maximum rate of liming.

Effect of soil fauna on pH

Soil invertebrates may affect pH directly, at the small scale of their gut contents, or at the scale of the whole soil profile by accelerating the incorporation of lime.

Most gut contents of invertebrates generally have neutral to basic pH. In the anterior gut of soil feeding termites, pH of up to 10.4 has been recorded, whereas values of 6.0 to 9.6 have been recorded in the medium and hindgut of higher termites (Breznak,

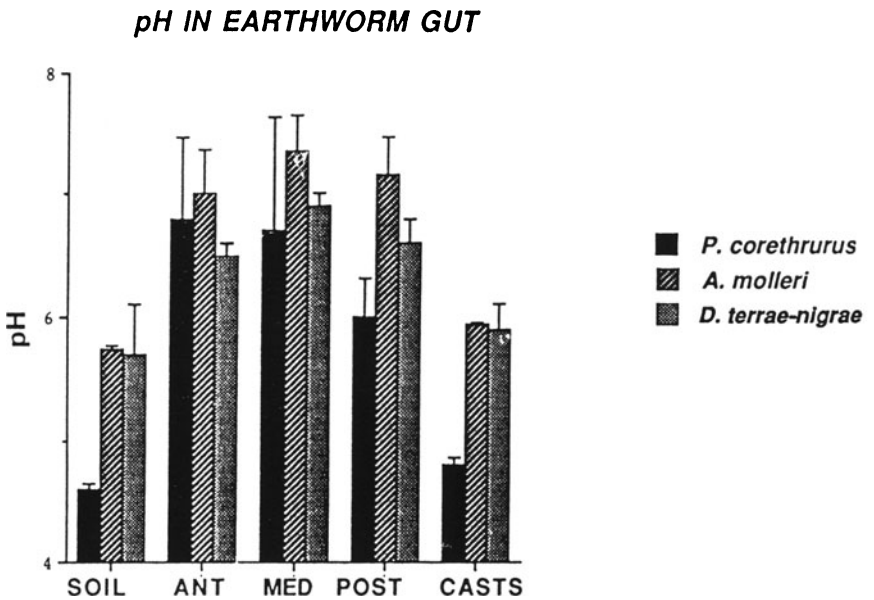

Fig. 7. Changes of pH during transit through the gut of endogeic earthworms and in fresh casts (Barois and Lavelle, 1986; Martin, 1988; Trigo and Lavelle, 1993). ANT = anterior gut, MED = median gut, POST = posterior gut.

1984). Similar values have been reported for earthworms. Measurement of pH in a control soil, three successive parts of the gut, and casts of three species of earthworms showed a significant increase of pH to neutral values in the gut. In the pantropical species *Pontoscolex corethrurus* pH increased from 4.6 to 6.6 but then decreased in the casts down to a value slightly greater than the control (Fig. 7). This temporary increase may have significant effects on soil processes which are sensitive to pH. For example, significant release of assimilable P has been observed in earthworm casts (Lopez-Hernandez et al., 1993; Brossard et al., 1995). Such effects are even more marked in the gut of some termites where pH of up to 13 has been recorded (Rouland et al., 1988). The large amounts of soil (up to 1000 t $ha^{-1}yr^{-1}$ or more) that may annually transit though the gut of termites and earthworms in some tropical soils, suggests that gut content may have significant impact on the soil profile.

In some cases, the pH of casts may increase significantly as a result of conversion of calcium oxalate crystals, found at the surface of ingested fungal hyphae, into calcium carbonate (Spiers et al., 1986).

Whole soil profile data are still limited. In New Brunswick, Canada, the invasion of virgin spodosols by two earthworms, one epigeic and the other one anecic, resulted in significant changes of the soil profile and pH of the Al horizon increased by up to 0.6 units (Langmaid, 1964). In culture soils of Peruvian Amazonia, the introduction of adapted earthworms did not result in any significant change of pH during six successive cropping cycles (3 years). In treatments with and without earthworms, pH first increased to neutral values as ashes were incorporated, but later decreased and fluctuated at values slightly higher than the original soil. The same lack of effect of earthworm introduction was observed with most parameters (Al saturation, P, SOM content) of chemical fertility (Pashanasi et al., 1992). Nonetheless, a significant increase of plant yield was observed in the presence of earthworms. In a continuous maize crop, increases of grain production of 40 to 300% were observed during the first three crops, in the absence of any application of fertiliser. From the third cropping cycle onward, fertiliser (NPK) was applied and at the 5th and 6th cycle grain production was still increased by almost 100% in treatments with earthworms.

Conclusion

Soil faunal communities are sensitive to acidity although different groups may react differently. Large invertebrates are more sensitive than smaller ones and, among them, arthropods are more acid tolerant than earthworms. As a result, acidification results in the

progressive elimination of large soil invertebrates, the most efficient ones with regard to activation of decomposition and participation to the formation and conservation of soil structure. Microfauna and mesofauna tend to be proportionally more important than in non-acid soil, but decomposition is slower. In such systems, faunal activity tends to be restricted to the litter system.

There is no evidence that acid soils have evolved specific faunas. Adaptation to the utilisation of low quality organic matter seems to have been the major driving force for evolution of soil invertebrates (Lavelle and Spain, 1995). Soil acidity may have indirectly influenced this evolutionary process since acid soils often produce low-quality plant material. Acid tolerant populations seem to have derived from a common pool of species which either have an improved tolerance for acidity, or simply colonise microsites with less acid conditions, such as the litter layer. This statement should be properly tested, especially for tropical earthworms and those groups of invertebrates which have been poorly studied in terms of the comparative ecology of sympatric species, starting with termites and the largest non-social arthropods.

Invertebrate communities seem to be more sensitive to acidity in temperate than in tropical soils. Endogeic earthworms have optimum distributions at pH 6 to 7 in temperate areas and 5 to 6 in tropical regions. This difference may be due in part to differences in the quality of litter produced. The poor quality of litter is partly responsible for the elimination of earthworms in temperate acid soils, frequently those with coniferous forests and associated low quality litter. The increase of earthworm densities following the application of high quality litter on acid soils supports that hypothesis (Huhta, 1979).

Correction of acidity by liming helps to develop active macroinvertebrate communities. Endogeic and anecic earthworms usually dominate these communities and populations of litter arthropods and Enchytraeidae are depleted. In tropical soils, liming is expected to have limited effects since soil faunal communities are largely acid tolerant. Coleoptera larvae which comprise a large number of severe pests, are an exception to that apparent rule since they seem to be affected by acidity.

There are clear indications that soil invertebrates, especially the largest ones, participate actively in the conservation of soil fertility through their influences on the dynamics of soil organic matter and on physical structure. These occur in a nested time and space relationship ranging from the smallest scale of a gut transit to a larger scale represented by bioaggregates and soil horizons. More research is necessary to extend our present knowledge and describe and quantify the participation of different functional groups of soil invertebrates in soil processes.

Management of organic residues seems to be the best way to promote activities of invertebrate populations which play a significant role in the conservation of soil fertility. Options which optimise these activities include (1) the production of high levels of biomass (stems, roots, leaves) to feed the invertebrates; (2) the association of different plant species (e.g. in alley cropping or agroforestry systems) to improve the overall quality of the organic resources and maintain biodiversity of soil fauna communities; (3) the use of organic residues available in the farming system (crop residues, coir, composted saw-dust, coffee residues); (4) a clever design of the size, shape and relative localisation of plots dedicated to different uses, in order to have "rich" plots in which soil fauna can grow and reproduce adjacent to "poor" plots (e.g. annual crop) which cannot sustain sufficient populations and need a constant flux of colonisers and (5) the use of selected acid tolerant key invertebrate species.

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